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Effects of Nutrient Enrichment and Water Motion on the Coral *Pocillopora damicornis*[1]

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ABSTRACT: Exposure of the hermatypic coral *Pocillopora damicornis* (Linnaeus) to elevated levels of dissolved inorganic phosphorus did not affect the colony or the zooxanthellae. Exposure to elevated levels of dissolved inorganic nitrogen and inorganic nitrogen + phosphorus led to an increase in algal density, and as a result, to an increase in the chlorophyll concentration. These latter two experimental enrichments slowed skeletal growth rate of the corals, probably because of a decrease in the photosynthetic rate of the algae and perhaps a decrease in the translocation of photosynthetic products from the algae to the coral. The algae probably used the photosynthetic energy for their own increased growth. Experimental manipulation of water motion used in these experiments did not affect the coral or the symbiotic algae.

CORAL REEF COMMUNITIES THRIVE in oligotrophic conditions because of the symbiotic relationship between corals and dinoflagellate algae (zooxanthellae). This symbiosis involves translocation of photosynthesized products, mostly reduced organic carbon, from zooxanthellae to host, as well as recycling of nutrients within the association.

Among the physical factors that control the growth, distribution, and abundance of corals is nutrient availability. Corals can take up, retain, and recycle both dissolved inorganic and organic nutrients (Muscatine and Porter 1977, Rahav et al. 1989). The coral *Stylophora pistillata* from the Red Sea responds to enrichment with ammonium or ammonium + phosphate mostly by increasing the algal density (Muscatine et al. 1989). Photosynthetic rate of nitrogen-enriched colonies increases compared with unenriched controls, although the photosynthetic rate per algal cell decreases (Dubinsky et al. 1990; McCloskey et al., in prep.). Addition of phosphorus to *Pocillopora damicornis* decreases the density of zooxanthellae (based on cellular C:N:P ratio), whereas addition of nitrogen did not have an effect on algal standing stock (Snidvongs 1987).

Water motion affects the rate of exchange of materials (including nutrients) across the coral-seawater interface and thus can influence respiration, photosynthesis, and calcification rates. In unstirred conditions net photosynthesis, respiration, and dark calcification of *Acropora formosa* were reduced compared to those of corals exposed to higher rates of water motion (Dennison and Barnes 1988). The growth, reproductive rate, and mortality of the hermatypic corals *Pocillopora damicornis* and *Montipora verrucosa* are also influenced by water motion (Jokiel 1978). Dennison and Barnes (1988) hypothesized that water motion affects coral metabolism by altering the thickness of the boundary layer adjacent to the animal tissue, thus altering diffusion rate of dissolved substances, particularly CO_2 and O_2. Diffusion rates may limit the rates of photosynthesis and calcification. Evidence of competition among algae for CO_2 was suggested by high algal densities in nutrient-enriched colonies of *Stylophora pistillata*. Photosynthetic rates on a per-algal-cell basis were inversely correlated with algal density, which increased in response to nutrient enrichment (Dubinsky et al. 1990).

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Because both nutrient concentration and water motion could influence nutrient uptake, we experimentally examined the influence of these factors on characteristics of the coral host, *Pocillopora damicornis*, and on characteristics of the symbiotic algae living in this coral.

TABLE 1

SYMBOLS USED FOR THE DIFFERENT TREATMENTS IN EXPERIMENT 1

MOTION	PHOSPHATE 0.1 μM	0.5 μM	2.0 μM
Control	LC	MC	HC
Slow	LS	MS	HS
Fast	LF	MF	HF

MATERIALS AND METHODS

Colonies of *Pocillopora damicornis* (Linnaeus), type "B" (Richmond and Jokiel 1984), about 10 cm in diameter were collected from the reef flat of Kaneohe Bay (Oahu, Hawaii).

Experiments were carried out in nine white fiberglass tanks with a water volume of ca. 400 liters (1.5 × 1.5 × 0.27 m). Each tank was supplied with unfiltered running seawater, at a rate of 4 liters min^{-1}. All tanks were aerated and exposed to full solar radiation.

Each tank was stocked with 21 to 24 colonies of *P. damicornis*. Before initiation of the experimental treatments, five or six colonies in each tank were stained with alizarin red at 20 ppm for ca. 12 hr. This treatment was used for determination of skeletal growth during incubation (Barnes 1972).

Experiment 1: Effects of Water Motion and Phosphate Enrichment

Stock solutions of KH_2PO_4 were continuously pumped into six of the tanks at a rate of 1 liter min^{-1}. The final concentration of PO_4^{-3} in three of the tanks was 2.0 μM, and in another three tanks was 0.5 μM. The concentration of the phosphate in three unenriched tanks was the same as in the surface water of Kaneohe Bay, 0.1 μM (Table 1).

Water motion was created by two means. All nine tanks were provided with aeration, which generated some water motion. Three of the tanks (controls) had only the water motion generated by this aeration. Water motion in the other six tanks (three slow water motion and three fast water motion) was enhanced by the up-and-down movement of a paddle in each tank. Each paddle was a 400-cm^2, square, weighted, horizontal plate located in the center of the tank. The paddles were lifted by a line connected through a pulley system to a modified shaker-table. The speed and amplitude of the movement of the paddles could be adjusted by altering the length of the lever arm on the table or the rate of movement of the table (Table 1). The water motion in the tanks was measured using clod cards as described by Muus (1968). The values of weight loss were as follows: control, 6.6 g; slow, 12.5 g; and fast, 16.5 g.

Phosphate concentration in the tanks was measured every 3 days according to Murphy and Riley (1962). Water motion was checked every 2 days.

Experiment 2: Combined Effects of Water Motion, Ammonium, and Phosphate Enrichment

Stock solutions of $(NH_4)_2SO_4$ and KH_2PO_4 were continuously pumped into seven ammonium-enrichment tanks and four phosphate-enrichment tanks. Final concentrations of NH_4 were 15 μM or 7 μM; final concentrations of phosphate, 0.5 μM. There were two unenriched tanks in which concentrations of these nutrients were the same as in Kaneohe Bay surface water, 2 μM ammonium and 0.1 μM phosphate.

Water motion in the tanks was created as in experiment 1. Four tanks had strong water movement; five tanks had only the water motion created by aeration (control) (Table 2).

Analytical Procedures

Every 3–4 days one colony from each tank was sampled randomly; Figure 1 summarizes the procedures. One branch from each colony

TABLE 2

SYMBOLS USED FOR THE DIFFERENT TREATMENTS IN EXPERIMENT 2

Ammonium level	2 μM	7 μM	15 μM	15 μM	15 μM
Phosphate level	0.1 μM	0.1 μM	0.1 μM	0.5 μM	2.0 μM
Water motion					
Slow	C	n	N	Np	NP
Fast	F	—	NF	NpF	NPF

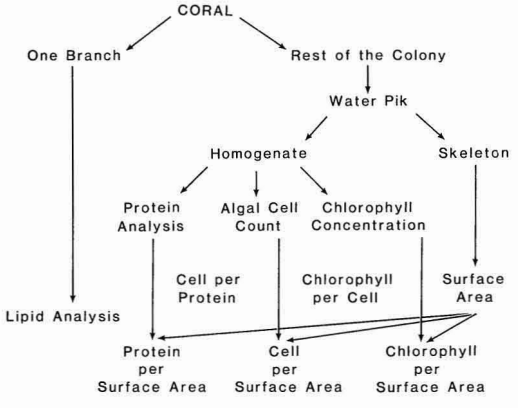

FIGURE 1. Summary of analytical methods.

was set aside for lipid analysis. The other measurements and analyses were done on the rest of the colony. Tissue was removed from the skeleton with a Water Pik (Johannes and Wiebe 1970). The volume of the homogenate was determined and samples were taken for determination of the following parameters: (1) number of zooxanthellae, using hemacytometer and light microscope; (2) concentrations of chlorophyll *a* (Jeffrey and Humphrey 1975); (3) protein analyses (Lowry et al. 1951); and (4) C:N ratio using an HP C:H:N analyzer.

The surface area of colonies was measured by immersing the corallum in hot wax. The mass of the wax added to the coral was determined by weighing the colony before and after immersion. A relationship between change in mass and surface area was obtained by immersing cubes of coral skeleton of known surface area into wax.

Calculations of the following parameters were based on the above measurements: (1) number of zooxanthellae per unit surface area; (2) chlorophyll *a* per unit surface area; (3) chlorophyll *a* per algal cell; (4) protein per unit surface area; (5) C:N:P ratio.

Linear growth rate of stained colonies was determined at the end of the experiment as the extension of branches beyond the red band deposited in the skeleton by the alizarin.

Analysis of variance (ANOVA) was used to compare the effects of the different treatments on the colonies. The Duncan-Waller test was used to compare treatment means.

RESULTS

Experiment 1: Effects of Water Motion and Phosphate Enrichment

The duration of the first experiment was 28 days. During the first 2 weeks algal density tended to decrease in all treatments and as a result the amount of chlorophyll *a* cm^{-2} decreased. During the second 2 weeks this trend reversed itself (Figure 2). The number of algal cells cm^{-2}, chlorophyll *a* cm^{-2} and chlorophyll *a* $cell^{-1}$ did not differ in corals exposed to different rates of water motion (Tables 3, 4, and 5).

Phosphate enrichment had no effect on the number of algae cm^{-2}, on chlorophyll per cell, or on chlorophyll cm^{-2} (Tables 3, 4, and 5). There was no noticeable effect of the different treatments on the protein level in the coral tissue (Table 6).

The increased phosphate concentration resulted in increased nitrogen content in the corals on one sampling day (25 July 1989) (Table 7); the C:P ratio was variable, ranging from 145 to 416 in the coral tissue (Table 8). There was no significant difference in growth rates of corals at different phosphate or water motion levels.

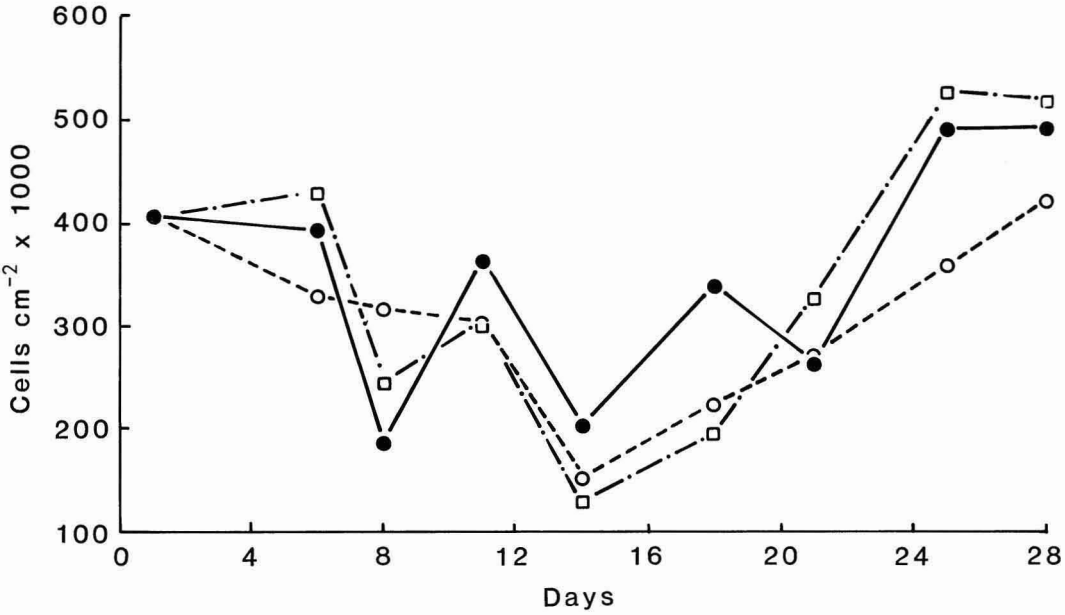

FIGURE 2. Effect of phosphate concentration on the number of zooxanthellae cm^{-2} in experiment 2. Each point represents the mean of three corals. □ = low, ● = medium, and ○ = high concentration.

TABLE 3

EFFECTS OF WATER MOTION AND PHOSPHATE ENRICHMENT ON CELL PER CM^2 IN EXPERIMENT 1

WATER MOTION	PHOSPHATE 0.1 μM L	0.5 μM M	2.0 μM H	MEAN
Control C	$6.12 \times 10^5 \pm 1.50 \times 10^5$	$3.85 \times 10^5 \pm 7.07 \times 10^4$	$3.50 \times 10^5 \pm 7.74 \times 10^4$	$4.49 \times 10^5 \pm 1.57 \times 10^5$
Slow S	$4.53 \times 10^5 \pm 2.57 \times 10^5$	$5.01 \times 10^5 \pm 1.27 \times 10^5$	$5.28 \times 10^5 \pm 5.20 \times 10^4$	$4.94 \times 10^5 \pm 1.71 \times 10^5$
Fast F	$5.05 \times 10^5 \pm 2.84 \times 10^5$	$3.25 \times 10^5 \pm 4.95 \times 10^4$	$6.06 \times 10^5 \pm 2.91 \times 10^5$	$4.79 \times 10^5 \pm 2.63 \times 10^5$
Mean	$5.23 \times 10^5 \pm 2.58 \times 10^5$	$4.04 \times 10^5 \pm 1.15 \times 10^5$	$4.94 \times 10^5 \pm 2.06 \times 10^5$	

NOTE: Means (±1 SD) for colonies from 25 July 1989 and 28 July 1989 after 21 and 24 days, respectively, of incubation.

TABLE 4

EFFECTS OF WATER MOTION AND PHOSPHATE ENRICHMENT ON CHLOROPHYLL PER CM^2 IN EXPERIMENT 1

WATER MOTION	PHOSPHATE 0.1 μM L	0.5 μM M	2.0 μM H	MEAN
Control C	2.194 ± 0.625	2.360 ± 1.024	1.372 ± 0.388	1.976 ± 0.846
Slow S	2.613 ± 1.131	2.353 ± 1.380	2.398 ± 0.653	2.455 ± 1.103
Fast F	1.919 ± 1.334	1.951 ± 1.109	1.652 ± 0.059	1.841 ± 1.011
Mean	2.242 ± 1.110	2.221 ± 1.196	1.807 ± 0.617	

NOTE: Means (±1 SD) for colonies from 25 July 1989 and 28 July 1989 after 21 and 24 days, respectively, of incubation.

TABLE 5

EFFECTS OF WATER MOTION AND PHOSPHATE ENRICHMENT ON CHLOROPHYLL PER CELL IN EXPERIMENT 1

WATER MOTION	PHOSPHATE 0.1 μM L	0.5 μM M	2.0 μM H	MEAN
Control C	3.630 ± 0.601	5.838 ± 1.652	3.872 ± 0.360	5.646 ± 1.432
Slow S	7.684 ± 3.519	5.633 ± 4.617	4.543 ± 1.077	5.953 ± 3.649
Fast F	5.594 ± 3.657	5.811 ± 2.732	4.059 ± 2.834	5.155 ± 3.199
Mean	5.636 ± 3.383	5.761 ± 3.242	4.158 ± 1.785	

NOTE: Means (±1 SD) for colonies from 25 July 1989 and 28 July 1989 after 21 and 24 days, respectively, of incubation.

TABLE 6

μG PROTEIN PER CM^2 IN EXPERIMENT 1

WATER MOTION	PHOSPHATE 0.1 μM L	0.5 μM M	2.0 μM H	MEAN
Control C	90.7 ± 56.3	29.3 ± 12.6	33.2 ± 6.6	51.1 ± 18.2
Slow S	64.2 ± 44.0	56.4 ± 33.4	42.6 ± 5.6	54.4 ± 20.0
Fast F	48.1 ± 11.9	36.1 ± 9.6	88.5 ± 19.7	57.5 ± 11.3
Mean	67.7 ± 19.4	40.6 ± 10.7	54.0 ± 6.4	

NOTE: Means (±1 SD) for three colonies at 25 July 1989 and 28 July 1989.

TABLE 7

C : N RATIO FOR ONE COLONY IN EXPERIMENT 1

WATER MOTION	PHOSPHATE LEVEL 0.1 μM L	0.5 μM M	2.0 μM H	MEAN
Control C	6.1	5.8	5.1	5.7
Slow S	7.1	5.2	4.8	5.7
Fast F	6.7	5.0	4.4	5.4
Mean	6.9	5.3	4.8	

TABLE 8

C : P RATIO FOR COLONIES IN EXPERIMENT 1*

WATER MOTION	PHOSPHATE LEVEL 0.1 μM	0.5 μM	2.0 μM
Control C	233	416	375
Slow S	145	238	345
Fast F	222	175	222

*Sampled on 25 July 1989 and 28 July 1989, after 21 and 24 days of incubation.

Experiment 2: Combined Effects of Water Motion, Ammonium, and Phosphate Enrichment

EFFECTS OF AMMONIUM ENRICHMENT. The second experiment ran for 13 days. The same decline in algal densities was observed in the colonies of the unenriched treatments. The algal density in the control (C) decreased from 1.24×10^6 to 4.66×10^4 and in the fast treatment (F) from 7.66×10^5 to 2.65×10^5. Coral colonies that were enriched with ammonium had significantly higher algal densities (1.55×10^6) than unenriched colonies (3.34×10^5) (Table 9). Although there were no large differences in the amount of chlorophyll per algal cell [6.190 (enriched) compared to 5.900 (unenriched) pg per cell] (Table 9), the chlorophyll cm^{-2} of enriched colonies was significantly higher than in unenriched colonies

(9.939 compared to 1.591 mg cm^{-2}) (Table 9). There was no clear effect of the treatment on the protein cm^{-2} (Table 9).

EFFECTS OF COMBINED PHOSPHATE AND AMMONIUM ENRICHMENT. Enrichment with ammonium and phosphate together caused an increase in the number of algal cells cm^{-2} compared to that of unenriched colonies and colonies that received only increased ammonium (Table 9).

Chlorophyll per unit area in colonies enriched with ammonium or ammonium plus phosphate was higher than that of the unenriched colonies (Table 9). The effect of the enrichment with ammonium alone on the concentration of chlorophyll cm^{-2} was similar to the effect of the combined nutrient enrichment (Table 9). There was no synergistic effect of water motion and of nutrient enrichment on the algal density (Figure 3).

TABLE 9

EFFECT OF WATER MOTION AND NUTRIENT CONCENTRATION ON ALGAL AND CORAL CHARACTERISTICS IN EXPERIMENT 2*

TREATMENT	cell/cm^2	chl/cm^2	chl/cell	Prot cm^{-2}
C	$1.96 \times 10^5 \pm 1.49 \times 10^5$	1.404 ± 1.012	7.714 ± 0.710	11.64 ± 3.20
F	$4.73 \times 10^5 \pm 2.08 \times 10^5$	1.778 ± 0.495	4.086 ± 0.751	19.07 ± 2.31
n	$2.61 \times 10^6 \pm 1.19 \times 10^6$	18.005 ± 9.647	6.593 ± 0.691	54.38 ± 30.07
N	8.99×10^5	5.381	5.984	16.13
NF	$1.16 \times 10^6 \pm 1.31 \times 10^5$	6.914 ± 0.726	6.118 ± 1.319	26.21 ± 5.41
Np	$1.95 \times 10^6 \pm 5.67 \times 10^5$	11.577 ± 2.841	6.022 ± 0.295	35.08 ± 17.56
NpF	$1.34 \times 10^6 \pm 4.20 \times 10^5$	7.659 ± 1.991	5.801 ± 0.334	25.98 ± 1.81
NP	$1.67 \times 10^6 \pm 6.71 \times 10^4$	10.853 ± 3.129	6.603 ± 2.145	28.90 ± 14.04
NPF	$1.48 \times 10^6 \pm 1.36 \times 10^4$	9.189 ± 0.509	6.210 ± 0.287	32.10 ± 8.32

*Colonies were sampled on 11 August 1989 and 14 August 1989 after 15 and 18 days, respectively, of incubation.

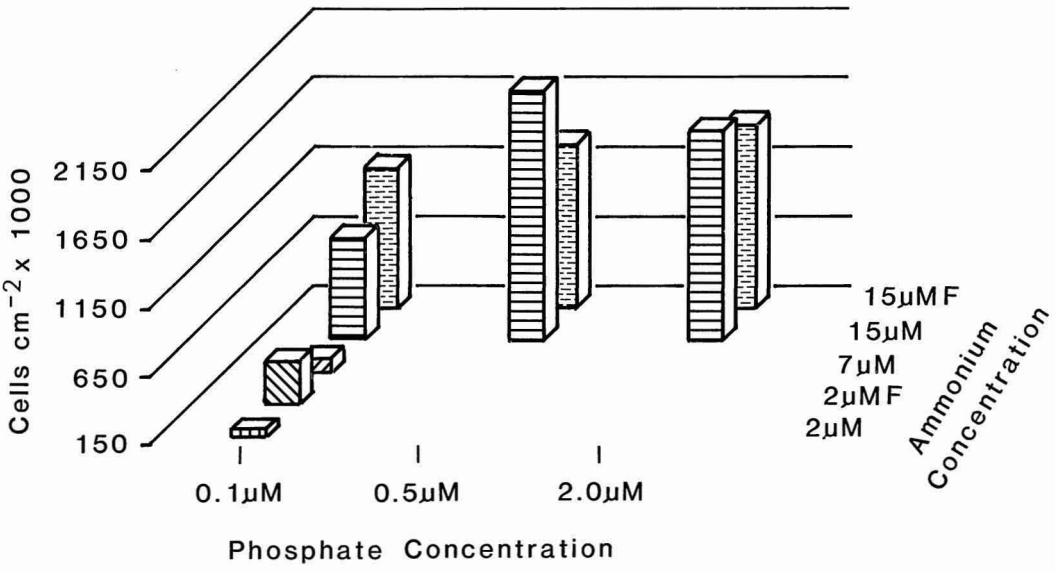

FIGURE 3. Effect of nutrient enrichment and water motion on the number of zooxanthellae cm^{-2} in the treatments of experiment 2. F stands for fast water motion; all other treatments had slow water motion.

Coral Growth

In all cases enrichment with 15 μM ammonium alone or ammonium plus phosphate reduced the skeletal growth rate of colonies during a 44-day period (Figure 4).

DISCUSSION

The results of this study show that ammonium enrichment has a greater effect on the coral *Pocillopora damicornis* than phosphate enrichment alone or water motion. There was a significant increase in algal density and decrease in the coral growth rate as a result of the ammonium enrichment. Colonies of *P. damicornis* that were supplied with 7 or 15 μM ammonium had more than twice the algae cm^{-2} compared to unenriched colonies (Table 9). The same phenomenon of increasing algal population was found when ammonium was added to colonies of the coral *Stylophora pistillata* from the Great Barrier Reef and from the Red Sea (Hoegh-Guldberg and Smith 1988, 1989, Muscatine et al. 1989, Dubinsky et al. 1990). It is possible that growth rate of zooxanthellae is limited by the amount of dissolved inorganic nitrogen in oligotrophic conditions (Hoegh-Guldberg and Smith 1989, Muscatine et al. 1989, Szmant et al. 1990). Addition of ammonium results in its uptake by algae, with an increase in algal cells cm^{-2} and chlorophyll cm^{-2}, but did not cause an increase in protein cm^{-2}. On the other hand, enrichment with 15 μM ammonium slowed down skeletal growth rate (Figure 4). The slower growth may be due to a reduction of translocation of photosynthetic products from the algae to the animal. Dubinsky et al. (1990) showed that photosynthetic rates calculated on a per-cell basis were inversely correlated with algal density. This means that the cell-specific contribution of zooxanthellae to the association decreased as their density increased. Reduction of translocation may occur if the algae use more of their photosynthetic products for their own growth. A decline in lipids in the enriched colonies (Stimson, unpublished data) could also be a result of the reduction in translocation. The slower skeletal growth may also be a reaction to the density of the algae, which may now compete for CO_2 that the coral uses for its calcification (Dubinsky et al. 1990). The difference in the linear growth of the skeleton between the control colonies and the ammonium-enriched colonies was 0.00778 cm day^{-1}. The difference between algal densities of control and enriched colonies at the end of the experiment [13 days (3.345×10^5 versus 1.58×10^6 cells cm^{-2})] indicates that the algal growth rate under enrichment was 9.57×10^4 cells cm^{-2} day^{-1} higher (assuming that the coral is a cylinder, diam. = 0.5 cm). This decrease in skeletal growth can explain ~100% of the increase of the zooxanthellae population.

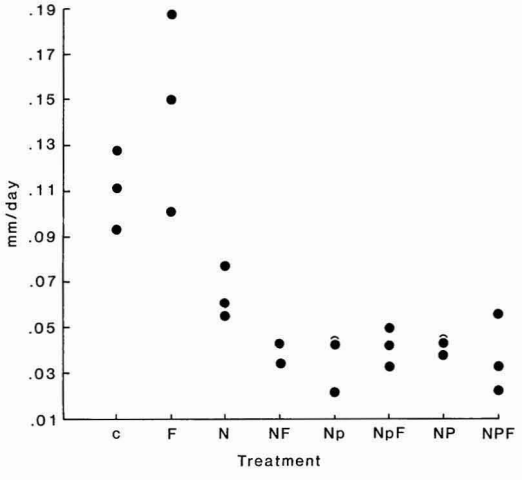

FIGURE 4. Linear growth of branch tips of *Pocillopora damicornis* in eight treatments over the 44-day period of experiment 2. Each point represents the mean growth of four tips per colony.

Addition of dissolved inorganic phosphate with or without a supply of ammonium did not affect algal density in these experiments or in that of Muscatine et al. (1989). This suggests that phosphate in seawater as well as in seawater enriched with ammonium is not a limiting factor for growth of zooxanthellae. It could be that continual enrichment with ammonium will ultimately cause a depletion of phosphate. Evidence for this is seen in the fact that colonies enriched with ammonium plus phosphate had higher algal density after 44 days of incubation compared to colonies with

ammonium alone (Stimson, unpublished data). The same results were observed by McCloskey et al. (in prep.) and Dubinsky et al. (1990).

Enrichment of *Stylophora pistillata* colonies with ammonium and ammonium plus phosphate caused an increase of chlorophyll *a* per algal cell (Muscatine et al. 1989, Dubinsky et al. 1990).

The increase of the chlorophyll *a* per cell may have been in response to increased shading among the algal cells due to their high density (Dubinsky et al. 1990). We did not see such a phenomenon in this experiment. The amount of chlorophyll per algal cell in enriched colonies of *Pocillopora damicornis* is not significantly different from that of the unenriched colonies (Table 9). It is possible that the high irradiance in this experiment, about 1000 μ Moles quanta m^{-2} s^{-1} at noon, reduced the importance of self-shading.

The amount of chlorophyll per unit coral area is dependent on the density of algae and their chlorophyll content. Colonies enriched with nutrients had more zooxanthellae and as a result more chlorophyll (Table 9), as seen in Muscatine et al. (1989) and Hoegh-Guldberg and Smith (1989).

Phosphate enrichment did not affect the chlorophyll concentration per alga.

Effects of Water Motion

Water motion at the three levels of this study did not affect the coral *Pocillopora damicornis* and its symbiotic algae. In this experiment there was no change in algal density or amount of chlorophyll cm^{-2} in the different water motion treatments. Neither was there a significant effect on skeletal growth rate of the coral. This result is in contrast to Jokiel's study (1978), which showed that water motion influences the growth, mortality, and reproductive rate of this hermatypic coral. The different results could be due to the difference in the incubation time, 70 days in Jokiel's experiment versus 13 and 28 days in our experiment, or to a difference in the level of water motion in the two experiments.

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